nonpairings of line and food from phase 1. More nonpairings resulted in slower acquisition of pecking to the white line. For each bird, key peck acquisition occurred within 20 trials for the novel stimulus. Since the acquisition rate for the novel stimulus was unrelated to the amount of differential conditioning, the retardation effect was specific to CS−.

Figure 2 shows the results of the combined-cues tests for groups 3 and 4. The mean response rates to the test stimulus are shown in comparison to the mean rates for the same number of randomly selected CS+ trials from the last session of phase 1. Similar response rates were controlled by CS+ in groups 3 and 4. Relative to CS+, the test stimulus totally suppressed responding for each bird in group 3. In contrast, the response rate to the test stimulus was similar to that of CS+ alone for group 4. The slight suppression of responding by the white line for group 4 could be due to generalization decrement. The results of the combined-cues tests show that the suppressive effect of the line for group 3 was due to conditioning factors.

The results of the retardation test together with those of the combined-cues tests show that an errorless S− can inhibit responding. Therefore, the occurrence of errors is not necessary for the establishment of S− as a conditioned inhibitor. These results strongly support the view that nonresponding to S− in errorless discrimination learning can result from inhibition by S−.

Since nonresponding to S− can result from inhibition by S− in learning with and without errors, the environment may not control behavior in qualitatively different ways in the two cases. A major problem for future study is whether similar environmental events produce discrimination learning with and without errors. Specifically, the role of such ubiquitous factors in discrimination training as the differential association of stimuli with reinforcement and nonreinforcement should be investigated. Comprehensive analyses of the behaviors that may be conditioned by such events (*6*) will be fundamental to the analysis of how the environment acquires control over an organism's behavior.

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Chimpanzee Spatial Memory Organization

Abstract. *Juvenile chimpanzees, carried around an outdoor field and shown up to 18 randomly placed hidden foods, remembered most of these hiding places and the type of food that was in each. Their search pattern approximated an optimum routing, and they rarely rechecked a place they had already emptied of food.*

This report describes the performance of young chimpanzees in a delayed response variation on the "traveling salesman" combinatorial problem (*1, 2*). In other applied sciences this problem is: Given the positions of several places on a scaled map, find the routing that will take you to all of these places with the shortest mileage. Here, the problem is: If a chimpanzee has in the past seen the locations of several hidden objects in a field, how does he manage to get to them again, and how does he organize his travel route? What does his iterinary tell us about the nature of his "cognitive mapping," his strategy, and his criteria of "efficiency" (*3, 4*)?

Six wild-born chimpanzees, 5 to 7 years old, were tested in the outdoor enclosure (30.5 by 122 m) in which they had lived as a group for more than a year. Their previous formal test experience (*5*) did not include delayed response tests involving multiple hidden goals; one animal (Bido) had had fewer than ten prior trials of any delayed response testing.

Before a trial began, all six animals were locked in a release cage on the periphery of the field. Then one experimenter took out a previously selected test animal and carried him about the field, accompanying a second experimenter who hid one piece of fruit in each of 18 randomly selected sectors of the field. Throughout this 10-minute process, the animal was not permitted to do anything other than cling to his carrier and watch the baiter; thus, primary reinforcement and locomotor practice during the information-gathering phase of a trial were eliminated (*6*).

After being shown the foods, the chimpanzee was returned to the group. The experimenters left the field, ascended an observation tower, and, within 2 minutes, pulled a cable that opened the release cage door. All six animals were released simultaneously and were free to roam. The five animals who had not been shown the food on a particular trial had no way to find the food other than through guesswork or cues such as odor, the behavior of the test animal, and inadvertent cues from the experimenters; thus, they served as controls for factors other than visual memory. The emotional dependence of the animals on each other precluded the possibility of testing each animal alone.

On a map that showed the location of each piece of food, the experimenters recorded the time at which each food pile was found or rechecked, and the identity of the animal involved. In addition, qualitative notes were made on behavior related to the search. Observation continued for at least 1 hour.

One trial was given each day for 16 days. Belle, Bandit, Bido, and Gigi each served as test animals on 4 trials and as control animals on the remaining 12 trials. Shadow and Polly were controls on all trials. On each trial the experimenters followed a different path and used a different set of 18 hiding places (*7*).

The animal that had been shown the food found a total of 200 pieces (12.5 per trial); the animals serving as controls found a total of 17 (0.21 per animal per trial). Usually, the test animal ran unerringly and in a direct line to the exact clump of grass or leaves, tree stump, or hole in the ground where a hidden food lay, grabbed the food, stopped briefly to eat, and then ran directly to the next place, no matter how distant or obscured by visual barriers that place was (*8*). His pace slowed as more and more food was obtained, and eventually he lay down for long rests; but he never wandered around the field as if conducting a general search. Control animals obtained food principally by searching around the test animal or begging from him directly. Only in four instances did a test animal manually search the ground more than 2 m from a food pile, as controls did on an uncountable number of occasions. It would seem that the major cue of food location was visual memory, and that the test animal did more than merely recognize each hiding place on the basis of local cues once he chanced to pass by that place.

Figure 1 shows each test animal's performance on the trial on which he found the largest number of foods. Each animal proceeded more or less in accordance with a "least distance" principle (*9, 10*), and with no regard for the pathway along which the experimenters had carried him. On the average, the itinerary of a given trial was only 64 percent as long as the mean of all possible $N!$ itineraries on that trial, and none of the 16 trials exceeded its chance-expected value (*11*). Extensive baseline data on the animals under routine nontest conditions indicate that the routes shown in Fig. 1 would be very unlikely if no animal had been shown the food. In fact, once they were habituated to the enclosure, the animals rarely traveled across it in an hour without some special incentive.

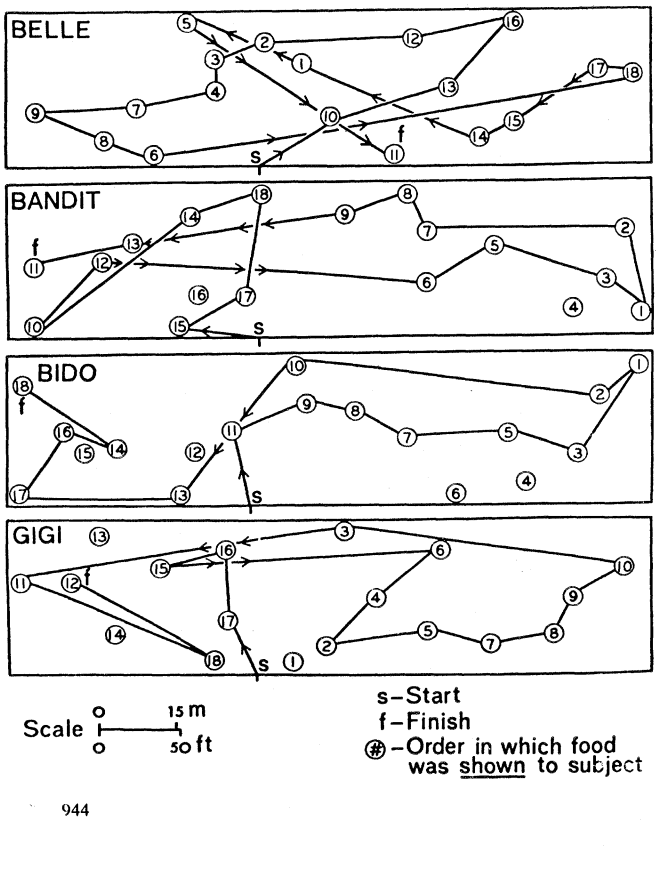
A second experiment tested whether the chimpanzees could remember the type of hidden food as well as its location. The same test procedure and animals were used, but now 9 of the 18 food piles contained a piece of nonpreferred food, vegetable, and 9 contained a piece of preferred food, fruit. The four test animals received three trials each.

The results were similar to those of the first experiment, except that on most trials the preference for fruit and the "least distance" strategy were additive determiners of choice. For example, in the first 9 responses of her first trial, Belle took 9 fruits (F) to 0 vegetables (V); Bandit, 7F to 2V; Bido, 7F to 2V; and Gigi, 4F to 5V; most of the remaining foods were taken later. (Only Gigi's preference for fruit on trial 1 was not significant by median test; and on subsequent trials she "corrected" this.) If the itinerary to fruits and the itinerary to vegetables are considered separately, each showed a fair "least distance" pattern.

It is unlikely that all 18 places were taken into account simultaneously at all times throughout a trial in these two experiments. On several occasions a test animal actually stepped on one pile of food on his way to another, and then, sometimes 10 minutes later, returned for it. Also, on several trials, a striking example of sudden recall occurred while an animal was apparently asleep. After having eaten many pieces of food and lain supine with his eyes closed for up to 30 minutes, the test animal suddenly jumped to his feet and ran 10 to 30 m straight to a hidden piece of food.

In only 11 instances (range 0 to 5 per animal) in these two experiments did a chimpanzee recheck a place that he had already emptied of food; thus, either memory of specific places was erased once reinforcement occurred, or the chimpanzees remembered where they had already been on a trial. Places that had already been emptied by another animal were, however, often rechecked.

A third experiment examined with a less complicated procedure the relative importance of "place" cues and "response" and route cues (*3, 4, 6*). The same test procedure and animals were used, but now only four food piles were shown on a particular trial, two on the left third of the field, 1, and



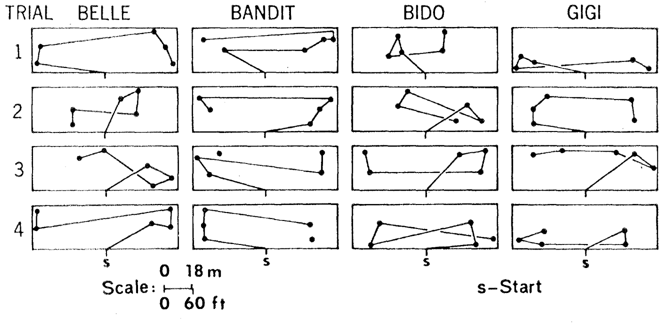


Fig. 1 (left). Maps showing each test animal's performance on the trial (out of four) on which he found the largest number of hidden foods in experiment 1. The connecting line gives an exact picture of the order in which the various places were searched, and a rough idea of the animal's general travel routes. (If the line touches a point, that point was searched.) Ecological details such as trees are omitted for clarity. Fig. 2 (right). Maps showing each test animal's first four trials in experiment 5. The connecting line gives an exact picture of the order in which the various places were searched and a rough idea of the animal's general travel routes. Since the release cage was not in the center of the X axis, and we wished to avoid biasing right or left positions, no food was placed to the extreme end of the longer (right) side. This portion of the field is not shown on these maps.

two on the right third, r. The exact locations varied from trial to trial, as did the order in which the four piles (l_1, l_2, r_1, r_2) were shown. In this experiment and subsequent ones the animals were tested in two independent trios (Shadow, Bandit, and Belle; Polly, Bido, and Gigi) rather than all together.

On none of 28 trials (7 per animal) did a chimpanzee go to the four foods in the same order we had shown them, or the reverse of that order. However, the results again indicated an acute memory of places and perception of relative distances. On all but two trials, the animals cleaned out both piles on one side of the cage, then went to the other two piles on the other side, and then quit. They followed an l, l, r, r sequence 14 times and a r, r, l, l sequence 12 times, and often used the shortest of all 24 possible itineraries.

A fourth experiment essentially replicated these last results on travel organization while the use of cues other than distant vision were restricted almost completely. All procedures were the same as in experiment 3 except that, instead of carrying the chimpanzee about the field, one experimenter held the animal directly in front of the release cage door while a second experimenter walked from one predesignated place to the next, held a piece of fruit aloft at each place, and dropped it in the grass. (It was not covered up further and was ordinarily visible from a few meters.) On the 13 trials in which the animals went to all four places, there were only three times that they failed to follow an l, l, r, r or an r, r, l, l sequence of travel. (The remaining 11 trials on which one or more foods was missed indicate some loss of information by comparison with experiment 3; but these trials tell one nothing about the principal question of how an itinerary between four points is organized.)

It remains possible that in the preceding tests the chimpanzees failed to take into account several places at the start of a trial, and instead recognized one of the nearest available places, went to it, looked about, recognized another goal location that was close to their present position, went to it; and so on. Therefore, we conducted a fifth experiment. It differed from experiment 3 in only one detail: two pieces of food were hidden on one third of the field, and three pieces were hidden on the opposite third of the field. On the null hypothesis, one would expect no preference for going first to the side with three pieces.

Figure 2 shows the results of each animal's first four trials. On 13 of 16 trials the chimpanzees went first to the side with the larger clustering of food. Thus, in addition to following a "least distance" strategy, they maximized the rate of food acquisition. In subsequent trials, the first-choice selection of the side with three foods declined slightly; but the overall results remain better than chance.

In summary, the chimpanzees appeared to directly perceive the relative positions of selected classes of objects and their own position in this scaled frame of reference (*12*). They proceeded on the strategy, Do as well as you can from wherever you are (*2*), taking into account the relative preference values and spatial clusterings of the foods as well as distances. If locomotor practice or primary reinforcement were necessary at all, it was before the experiments began—which renders these variables of greater developmental than structural interest (*13*). Although it is unlikely that the animals "sorted over" all *N*! possible routes before making their first move, or that "space" as they perceived it can be compared literally to a picture on a piece of paper, their achievements are a good first approximation of those at which an applied scientist would arrive from his real maps, algorithms, and a priori criteria of efficiency. Mentalistic terms such as "cognitive mapping" do not necessarily explain the above facts, but they predict them accurately and describe them succinctly. Especially in the light of other recent research (*5, 14*), one is struck again by the parallels between chimpanzee and human behavior, the necessity for including representational processes in any adequate formulation of learning and memory, and the apparent evolutionary independence of representational ability and verbal language.

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8. If food was not located within 5 m of a distinctive landmark (such as a tree), the chimpanzees more often slowed down when they came within a few meters, and visually scanned the ground. In all of these experiments the animals' most common error was to search a grass clump, dead branch, or other features that looked (to us) almost precisely like the correct hiding place, and was within a few meters of it. I would speculate that, like human beings, the chimpanzees used a hierachy of visually perceived object-relations for determining an exact location. In the cue-giving phase of the experiment, one initially had the impression that they did not even attend to the food (unless it was held up to their mouth). Instead, they glanced once at the hiding place and then looked up toward a tree or around the field, as if to first locate the position of food relative to a local cue and then locate the position of that local cue with respect to some landmark or the field in general.
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